

epitome of a coal-seam: its roots represent the *Stigmaria*-underclay; its bark the compact coal; its woody axis the mineral charcoal; its fallen leaves (and fruits), with remains of herbaceous plants growing in its shade, mixed with a little earthy matter, the layers of coarse coal. The condition of the durable outer bark of erect trees concurs with the chemical theory of coal, in showing the especial suitability of this kind of tissue for the production of the purer compact coals. It is also probable that the comparative impermeability of the bark to mineral infiltration is of importance in this respect, enabling this material to remain unaffected by causes which have filled those layers consisting of herbaceous materials and decayed wood with pyrites and other mineral substances."

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XLI.—*On the Limits and Classification of the Ganoids.*

By Dr. C. LÜTKEN\*.

IN my memoir on the limits and classification of the Ganoïdei (Om Ganoidernes Begrændsning og Indeling, Copenhagen, 1869) my only object was to summarize and expound the results at which science has arrived with regard to the important question above indicated; and its importance, whatever this may be, is due solely to the necessarily restricted number of those who have had the time, patience, and leisure to become thoroughly acquainted with these results by their own investigations. Certainly the history of palæichthyology shows very plainly that hitherto this question has not been perfectly clear, in part because several of the most eminent authors have, unfortunately, been unable to obtain an exact knowledge of the works of their predecessors. Hence, at least in part, arises the uncertainty as to the definition and limits of the Ganoïdei, the rank which they should occupy in the zoological scale, the mode of subdividing them, &c. Have we not seen Andreas Wagner, whose memoirs on the fishes of the Lithographic Limestone constitute one of the greatest triumphs of palæichthyology, contenting himself with a definition applicable only to a particular formation? and Rodolph Kner, the learned describer of the fishes of ancient and recent times, expressing the opinion that, at bottom, there are no Ganoids at all, and that the forms united under this name are nothing but the prototypes of the different existing ichthyological families, having nothing in common but a character of antiquity? England and southern Germany have been the prin-

\* Translated by W. S. Dallas, F.L.S., from the 'Bibliothèque Universelle,' March 15, 1871, Arch. des Sci. pp. 283-296.

cipal modern centres of palæichthyological investigations; but (speaking, however, of a time which already belongs to the past), unfortunately, the English authors have generally had but little knowledge of the works of their colleagues on the shores of the Danube, and *vice versâ*. Thus the important and excellent memoir of Prof. Huxley on the classification of the fishes of the Devonian system, a work truly marking an epoch in palæichthyology, has remained almost unknown on the Continent.

The first portion of my work is exclusively of an historical and critical character, and will only be mentioned here very briefly, although it serves as the basis of the following part. Passing in review the more or less important writings\* of Agassiz, Johannes Müller, Stannius, Gegenbaur, Williamson, Kölliker, Heckel, Wagner, Huxley, Kner, &c., I have shown that no one has ever been able to give an exact definition of what is a Ganoid, neither the external or so-called zoographic characters, nor those borrowed from anatomy and histology (*i. e.* the microscopic examination of the scales) having been capable of remedying this defect. The restricted space which you will devote to this summary will, however, prevent me from expressing my opinion upon all the points of the external and internal structure of these animals, to which more or less importance has been ascribed, with more or less justice, in connexion with their classification. I shall abide by the testimony of the late Dr. Kner, who said with so much reason that it will be impossible to give any definition of the order Ganoidei if we desire to maintain the limits which are generally assigned to it; and I also take my place on his side when he proposes subsidiarily to restrict its limits and to reduce it from the rank of a subclass or order to a lower place in the systematic scale. But I am far from being able to approve of his principal proposition of striking this tribe completely out of the zoological system—a proposition which is not supported by any indication as to the eventual distribution of this great group of diverse types among the other suborders of the class of fishes, and which, as we shall soon show, would be quite contrary to nature.

The theoretical or constructive method, that of zoographic or zootomical characters, having therefore failed, it will be necessary to apply to this question the *synthetical* or comparative method, a work of labour and patience, it is true, but always leading with certainty to the goal,—that is to say, the method which consists in ranging the known types in accord-

\* At the end of my memoir there is a list of the principal publications upon this division of ichthyology, from 1841 to 1869.

ance with their affinities and the totality of their characters, species by species and genus by genus, until the families are formed; and then, by bringing together the families in the same manner, without any preconceived idea, we shall succeed by degrees in establishing groups of a higher order, and finally see rise before us the true natural system, the subdivisions of which will rest upon the solid basis of experience and the totality of the facts. We must therefore, provisionally at least, limit the name of Ganoids to the indubitable existing types (that is to say, the *Lepidostei* and *Polypteri*), and to the fossil types which will naturally group themselves around these, by giving proofs of their affinity rendered incontestable by the absolute concordance of important characters; whilst we must in the same way eliminate, at least provisionally, all the forms between which and the preceding our comparative synthetic method shall prove incapable of establishing any bond of relationship. The picture which the suborder Ganoidei will present to us after a scrupulous investigation of this kind will be nearly as follows:—

I. First series.—The *Lepidosteidae* or *Euganoidei* will include the fishes with bony, enamelled, rhomboidal, and articulated scales, related to the existing *Lepidostei*, and possessing neither the dermal ribs of the *Lepidopleuridae*, nor the fringed or oar-like paired fins of the *Polypteridae*, nor the gular plates which take the place of the branchiostegal rays in the latter\*. Although apparently forming a very natural group, there is no positive peculiarity which characterizes these in an absolute and exclusive manner. As regards the scales of the body, they possess characters common to a portion of the *Polypteridae*; the so-called *fuleral* scales of the margins of the fins, which occur at least in the majority of the fossil *Lepidosteidae*, occur also in the ancient *Lepidopleuridae*, and even in some true *Teleostei* of the Jurassic period; leaving out of consideration the living *Lepidostei*, the fossil *Lepidosteidae* appear to have had a common character in the delicate and numerous rays of the fins and branchiostegal membrane; lastly, the forward position of the ventral fins upon the middle of the belly will also distinguish them from the *Polypteridae* with similar scales.

Although this series embraces a very great number of genera, the greater part of which will be found mentioned in my memoir, it seems to me to be impossible to subdivide it naturally into tribes or families. We might perhaps distin-

\* With the sole exception of *Cheirolepis*, the only Devonian type of the whole series which indicates by its gular plates a certain relationship to the contemporaneous *Polypteridae*.

guish between the genera with large and those with small scales, and between the heterocercal and subhomocercal types; and in this way we should obtain a quaternary division such as this:—

- |    |              |             |               |       |                         |
|----|--------------|-------------|---------------|-------|-------------------------|
| 1. | Lepidosteidæ | heterocercæ | microlepidotæ | ..... | <i>Cheirolepis.</i>     |
| 2. | „            | homocercæ   | „             | „     | ..... <i>Sauropsis.</i> |
| 3. | „            | heterocercæ | macrolepidotæ | ....  | <i>Paleoniscus.</i>     |
| 4. | „            | homocercæ   | „             | „     | ..... <i>Lepidotus.</i> |

But it appears to me to be impossible to mark out fixed limits between these groups, which are artificial rather than natural. It has also been proposed to divide the *Euganoïdei* into “monostichi” and “distichi,” according to the single or double arrangement of the scales bordering the fins; but we are still destitute of sufficient information to enable us to adopt this classification, even if it has an actual foundation in nature.

Every one knows that there is a difference of epoch between the *Euganoïdei* called “heterocercal” and those called “homocercal,” or, better, “simorrhachal;” but the line of demarcation is not so clearly drawn as has been supposed. As early as the Permian system there are species (referred to the genus *Paleoniscus*) which are only semiheterocercal, whilst in the Lias we may still find absolutely heterocercal genera (*Orygnathus*, *Cosmolepis*). In general, however, an evident progress from the heterocercal to the so-called homocercal or fan-like tail may be observed running parallel to the progress of geological epochs. A similar progress is marked also, although perhaps less distinctly, in the structure of the vertebral column. No Lepidosteid presents true biconcave vertebral bodies: except in the living *Lepidostei*, we find either a *naked notochord* without any trace of vertebral bodies, the apophyses of the vertebræ, the interapophysial bones, the scapular arch, the fin-rays, &c. being at the same time well developed and ossified; or *semivertebræ*, that is to say, superficial plates, derived from the neurapophyses and hæmapophyses, covering the notochord completely or partially, and frequently, by touching or covering each other, simulating false vertebræ; or, lastly, these plates becoming amalgamated, so-called *annular vertebræ*, differing, however, from the true vertebræ of fishes by their smooth surface and their bony interior enclosing the notochord, almost completely developed. The reader who may wish to have more ample information upon this subject I recommend to consult especially the works of MM. Heckel and Wagner.

II. Second series.—The *Lepidopleuridæ* or *Pycnodontes* are

especially characterized by peculiar dermal ribs\* which protected their sides, at least on the anterior part of the body, and which held suspended the scales, which are sometimes very delicate, and are rhomboidal, and not articulated, but interlocking in a very peculiar manner. Generally there is also something very characteristic in the form of the body, which enables us at once to distinguish this well-marked and very remarkable *extinct* type. If we knew only its most recent representatives, we might doubt as to their true position in the system, so widely do they depart from the Euganoid type; but there is an uninterrupted series, leading directly from the Eocene Pycnodonts to the Palæozoic *Platysomi*, which no one has ever thought of excluding from the Ganoidei, and showing evidently the filiation of all these creatures. It is a peculiar branch which separated during the Carboniferous period from the common trunk of the Ganoids, and continued in the course of time to depart more and more from its starting-point, to become developed in a more and more perfect manner, and to spread out into a multitude of well-marked genera, until it reached the term of its existence during the Eocene period. The classification of the *Lepidopleuridæ* will reproduce before us the image of this zoological progress:—

a. The Palæozoic *Lepidopleuridæ* or *Platysomii*, with the scaling of the body and the dermal ribs completely developed, with fuleral scales bordering the fins, with a naked notochord, and semivertebræ but slightly or not at all developed, &c. *Platysomus* and allied genera belong to the Carboniferous and Permian formations.

b. The Liassic *Pleurolepididæ* differ from the *Stylodont Platysomii* only by their well-marked homocercity.

c. The *true Pycnodontes* of the Jurassic, Cretaceous, and Tertiary periods are also homocercal, but the fuleral scales are wanting; the semivertebræ are more or less perfectly developed. Their very characteristic and diversified dentition furnishes excellent generic characters.

α. The *Mesozoic Pycnodonts* had the notochord partly naked, the development of the semivertebræ being less perfect. The dermal ribs in some formed a trelliswork all over the body as in the preceding, in the others only on the anterior part, as in the following.

\* I have here followed the opinions of M. Heekel with regard to this part of their organization. According to Sir P. Egerton, these dermal ribs are only the anterior and thickened portion of the scales. In the question of classification, with which we are here occupied, this difference is of little importance; the character is persistent, even if the mode in which it has been expressed should prove to be false.



β. The *Neozoic* (Eocene\*) *Pycnodonts* had the semivertebræ developed, and consequently covering the notochord entirely; the dermal ribs, which are sometimes delicate and complicated, never occupied more than the thoracic portion of the body.

III. Third series.—The *Ganoïdei Crossopteri* or *Polypteride*, represented in the present day by the genera *Polypterus* and *Calamoichthys*. The principal characters common to these and their ancient representatives of the Devonian system are the following:—1, the absence of rays in the branchiostegal membrane, which are represented here only by two gular plates; 2, the very characteristic structure of the paired fins, which are formed of a scaly stem, often of great length, and bordered on each side with rays like a fringe; 3, the very backward position of the ventral fins; 4, the absence of the so-called fuleral scales; 5, the diphyocercal or approximately heterocercal form of the tail, which is never fan-like.

The true *Polypteride* of the existing period are the direct representatives of the Palæozoic *Rhombodipteri* (Devonian and Carboniferous) with ossified, rhomboidal, and articulated scales like those of the *Lepidostei* and *Polypteri*, with a diphyocercal or slightly heterocercal tail, with a double dorsal fin thrown far back, with the base of the vertical fins scaly, &c. The principal character which separates them from the *Polypteride* therefore consists in the double dorsal placed far back. These are the genera *Osteolepis*, *Diplopterus*, *Megalichthys* (with smooth scales), *Glyptolemus* and *Glyptopomus* (with the scales and bones of the head sculptured).

The contemporaneous *Cyclodipteride* present exactly the same assemblage of characters, with one single exception—that of the scales: these are ossified and enamelled, indeed, and sometimes even thick and smooth or sculptured, as in the preceding; but in place of the form, relative position, and articulation common to the *Euganoïdei*, *Rhombodipteride*, and *Polypteride*, we find here the rounded *cycloid* form and the imbricated superposition of the ordinary *Teleostei*. As among the *Rhombodipteride*, there are among the *Cyclodipteride* a smooth division (*Ctenodus*, *Dipterus*), and another with the cranium and scales sculptured (*Glyptolepis*, *Holoptychius*, *Gyroptychius*, &c.).

In a certain number, at least, of these *Dipteride*, whether rhomboidal or cycloid, if not in all, the vertebral column already possessed apparently a degree of development little, if at all, inferior to that of the *Polypteri* of the present day; in

\* A single species of this tribe is obtained from the Cretaceous formation of Lebanon. For further details concerning the true *Pycnodonts*, their structure and classification, the reader will consult especially the celebrated works of the late M. Heckel.

other allied genera, such as *Phaneropleuron*, a Devonian genus differing from the *Cyclodipteri* by its undivided dorsal fin occupying the posterior half of the back, a naked notochord is combined with ossified ribs, apophyses, and rays, as in the ancient *Lepidosteidae* and *Lepidopleuridae*.

The great extent of time which separates the Palæozoic *Dipteridae* from the living *Polypteridae* is filled up in part by the remarkable group of the *Cælacanthi*, presenting a very peculiar combination of unique zoological and anatomical characters (for example, the structure of the tail, the peculiar interspinals of the anal fin and of the two dorsals, the ossified swimming-bladder, &c.), with less anomalous features borrowed from the other *Ganoidei Crossopteri* (such as the gular plates, the fringe-like paired fins, the scaly base of the vertical fins, the duplicity of the dorsal, &c.). This group originated in the Carboniferous period, and maintained itself with rare persistence of type throughout all geological periods down to the Cretaceous, when it became extinct. But as I can refer the reader to the admirable works of Prof. Huxley, to whom belongs the inestimable merit of having so perfectly seized and so admirably developed the relations of the different types belonging to the great polymorphic series of the *Ganoidei Crossopteri*, I shall abstain from speaking of them at greater length, so as to abridge this summary as much as possible.

Here concludes the representation of the *true Ganoids*, as to the nature of which there is no doubt, thanks to our method of synthesis. But what is to be done with all the other types which have been referred to the Ganoids by a greater or less number of authors? I will not speak here of the *Siluroidei*, which are true Physostome Teleosteans, nor of the *Lophobranchii* and *Plectognathi*, belonging to the suborder of Aphysostome Teleosteans, nor of the *Dercetiformes* or *Hoplopleuridae*, a very remarkable tribe characteristic of the Cretaceous period, if we omit the Triassic genera *Belonorhynchus* and *Ichthyorhynchus*, the place of which in the system is uncertain (perhaps they ought to be arranged among the *Aphysostomi*), but which have no relationship to the *Ganoidei*. But I must express a more decided opinion upon the other types generally regarded as Ganoids—namely, the *Lepidosirens*, the *Sturgeons*, the *Amiidae*, the Jurassic *Teleostei*, the *Acanthodei*, and the so-called *cuirassed Ganoids*—types to which I have not yet been able to assign a place in the picture of the Ganoids, seeing that the synthetic method has not yet proved those intimate bonds, those relations of structure, those intermediate forms—in one word, that filiation which alone would allow us to place them there. Nevertheless we must not deny the possi-

bility that future discoveries may some day demonstrate to us these still unknown bonds\*; nor must we forget that it is not many years since naturalists did not hesitate to refuse a place among the Ganoids to the *Aspidorhynchi*, the *Cœlacanthi*, and the *Pycnodontes*, which we now arrange without hesitation among the undoubted Ganoids.

a. In the first place, the *Lepidosirens* or *Protopteri*, classed by some writers of incontestable authority with the Ganoids, but most frequently regarded as forming a peculiar subclass (*Dipnoi*), will form, in my opinion, only an aberrant tribe or a suborder of the Physostome Teleosteans, to be placed in the immediate vicinity of the Ganoids and particularly of the *Crossopteri* (*Phaneropleuron*, for example).

b. Then the *Sturgeons* are also Physostome Teleosteans, which should be arranged as near as possible to the *Chondrostei*, between the latter and the *Ganoidei*, with which, however, they must not be united †.

c. The *Amie* approach the Ganoids and Chondrosteans by a number of remarkable anatomical peculiarities; but we should not be more justified in classing *Amia* with the Ganoids than in arranging the Sturgeons among the Selachia. It is a special type, belonging to the true Physostome Teleosteans, leading towards the Ganoids, but not attaching itself to them. Moreover the removal of this group from the suborder Ganoidei will but slightly modify the palæichthyological system, as it includes only a small number of forms (*Notus*, *Cyclurus*, *Amiopsis*), which perhaps ought to be united with *Amia* itself.

d. There is also no positive reason for arranging the *Jurassic Teleostei* (*Leptolepides*, *Megaluri*, and *Caturi*) either with the Amiidæ or with the Ganoidei. If we consult the synthetic method, it will lead us rather towards the *Halecoïdes*—that is to say, the Salmons, Herrings, and *Clupesoces*. They are consequently true Physostome Teleosteans, and, with the exception of the *Belonorhynchus* &c. of the Trias, the most ancient representatives of this suborder. Moreover it will be impossible to separate the three families above named from each other; those who, with the modern palæichthyologists, Heckel, Wagner, and Pictet, place the *Leptolepides* among the true Teleostei, will be obliged likewise to place there the *Megaluri* and *Caturi*, notwithstanding the fulcral scales bordering their fins; the filiation of the species, the crossing of

\* At this moment the journals inform us of the discovery in Australia of a new genus of freshwater fish, intermediate between the *Lepidosirens* and the Palæozoic *Dipteri*! [See papers by Dr. Günther and Messrs. Hancock & Atthey in the March Number of this Journal.—ED. *Ann. Nat. Hist.*]

† The affinities of the fossil genus *Chondrosteus* are perhaps still doubtful.



characters will leave them no choice. The *Leptolepides* and *Megaluri* have the true biconcave vertebræ of the Teleostei; but there is nothing astonishing in the fact that there was among the most ancient Teleostei a type (the *Caturi*) with a more embryonic spinal column—that is to say, with “annular vertebræ” or “semivertebræ.”

*e.* If the *Acanthodei* should be classed with the Ganoids, they will undoubtedly form a separate division; but I am rather of the opinion of those authors who regard them as a special type among the *Chondrostei*. The reader will consult with advantage the excellent exposition of this question given by Prof. Huxley in 1861. Lastly, whether we regard this remarkable family as the group of Ganoids most nearly approaching the Selachia, or as the Selachian type nearest to the Ganoids, is not of much consequence in reality.

*f.* Finally, with regard to the *Placodermi*, I must in the first place declare that I do not understand why so much stress has lately been laid upon the profound diversity of type between the *Cephalaspides* on the one hand, and the *Coccostei* (with *Pterichtyus*) on the other. Prof. Huxley regards the latter as true Teleostei, and places the *Cephalaspides* provisionally with the Sturgeons, at the same time indicating their analogy with the *Siluroïdei*. In my opinion, these are all animals of uncertain position, “*incertæ sedis*,” the true affinities of which still remain to be discovered. If we are still to persist in regarding them as “*cuirassed Ganoids*,” it will be necessary to establish for them a special division (fourth or third) in the suborder of Ganoids.

*What, then, is a Ganoid?* If it is absolutely necessary to give a definition, it must be formulated nearly as follows:—*Every fish* (abdominal, malacopterygian, physostome) *with osseous scales, articulated* (as in the *Lepidostei*) *or interlocked* (in the manner of the *Pycnodonts*), *or with gular plates in place of the branchiostegal rays, and with the paired fins fringed and scaly* (as in the *Polypteri*), *or which combine several of these characters, will be classed among the Ganoids*\*. And with regard to the position and rank which the Ganoids should occupy in the system, it will be necessary to form with them a suborder of the Physostome Teleostei, touching upon the *Chondrostei*, but separated from these by the Sturgeons, and surrounded by the Jurassic Teleostei, the *Amiidae*, and the

\* Even if we should prefer to suppress the suborder *Ganoïdei* altogether, and to place the three families *Lepidosteidae*, *Lepidopleuridae*, and *Polypteridae* after the *Siluri*, *Characini*, *Cyprini*, *Salmones*, and the other physostome families, the term “Ganoid” must still be regarded as a general denomination for these three families, which are so intimately connected.

*Protopteri*. The table of that portion of the ichthyological system with which we are here occupied will then present nearly the following aspect:—

Subclass I. *Teleostei Eleutherobranchii*.

(*Osseous Fishes with free branchiæ.*)

Order I. *Physoclistes* or *Acanthopteri* (including the *Acanthopteri*, *Anacanthini*, and *Pharyngognathi* of Johannes Müller, groups which cannot be maintained; and, besides these, the *Lophobranchii* and *Plectognathi*, which must be reduced to the rank of simple families).

Order II. *Physostomi* or *Malacopteri*.

Suborder I. The typical *Physostomi* (corresponding to the *Physostomi* of Johannes Müller, with the addition of the *Amiidae* and the *Leptolepides*, the *Megaluri*, and the *Caturi* of the Jurassic period).

Suborder II. The *Ganoidei*.

Series 1. The *Lepidosteidae* or *Euganoidei*.

Series 2. The *Lepidopleuridae* or *Pycnodontes*.

Fam. 1. The *Platysomi*.

Fam. 2. The *Pleurolepides*.

Fam. 3. The true *Pycnodontes*.

Series 3. The *Crossopteri* or *Polypteri*.

Subseries 1. The *Crossopteri Rhombiferi*.

Fam. 1. The *Polypteri*.

Fam. 2. The *Rhombodipteri*.

Subseries 2. The *Crossopteri Cycloidei*.

Fam. 1. The *Cyclodipteri*.

Fam. 2. The *Phaneropleuri*.

Fam. 3. The *Cælacanthi*.

Suborder III. The *Lepidosirens* or *Protopteri*.

Suborder IV. The *Sturgeons* or *Acipenseridae*.

Subclass II. *Chondrostei Desmobranchii*.

(*Cartilaginous Fishes with fixed branchiæ.*)

Order III. *Selachii*.

Suborder 1. The *Acanthodei*.

Suborder 2. The *Pleuracanthii*.

Suborder 3. The *Chimærii*.

Suborder 4. The *Sharks*.

Suborder 5. The *Rays*.

Order IV. The *Cyclostomi*.

Order V. The *Branchiostomi*.

*Incertæ sedis.*

Order VI. The *Placodermi* (*Cephalaspis* &c.).

In concluding this abridgment, which is certainly too short to enable the reader to judge as to the justice of my opinions, but may perhaps suffice to give an idea of them, I will add one or two words—namely, that my memoir is illustrated with fourteen woodcuts representing the figures, in part restored, of the principal types of the palæichthyological system, and also that the ichthyological table annexed to it, when compared with that in the great work of Prof. Agassiz, will furnish the means of seizing at a glance the principal progress made in palæichthyology from 1843 to 1869.

XLII.—On a new Species of Lemur from Madagascar, and on the Changes of Lemur macaco, Linn. By Dr. J. E. GRAY, F.R.S. &c.

*Prosimia rufipes*, n. sp.

Fur woolly, thick, dark rufous brown, with a golden gloss from the tips of the hairs; the sides of the head and cheeks, the hand and arm, and the feet and the sides to the under part of the body bright bay. Tail nearly black, rather longer than the head and body. Male with the middle of the throat greyish; face with short blackish hair. Female similar above, but with the chin, throat, and front half of the under part of the body reddish grey; the face and edge of the under jaw covered with blackish hairs.

*Hab.* Madagascar (Mr. Crossley). B.M.

With these two Lemurs were received a series of *Varecia varia* and *V. rubra*, showing that they are one species, extremely variable in colour; but, as far as I have observed, the head, the underside of the body, limbs, the feet, and tail are black, the back of the neck and the base of the tail are always white, while the colour of the back varies from dark red-brown through all gradations to pure white. In most specimens the shoulders, the sides of the chest, and the outside of the thighs, are the same colour as the back; but in one specimen these parts are deep black like the underside of the body. I might have been inclined to consider this variety to be a distinct species, as I believe it has been considered (*Lemur macaco*, Linn.); but one of the nearly white specimens has the base of the white hair of these parts black and partly showing through the white fur, and the white hairs of all parts of the body have a black base.

This series shows that *Lemur macaco* and *Lemur ruber* and *niger* of Geoffroy are one species.